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# Negative responses of ecosystem autotrophic and heterotrophic respiration to experimental warming in a Tibetan semi-arid alpine steppe

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ABSTRACT

Evaluating the responses of ecosystem respiration (Re) and its components to climate change is crucial for predicting terrestrial carbon cycling, particularly for the alpine grassland ecosystems. However, effects of climatic warming on ecosystem heterotrophic respiration (Rh) and autotrophic respiration (Ra) remain poorly understood in semi-arid alpine grasslands. A field manipulative experiment was conducted to investigate the effects of experimental warming on total Re, Rh and Ra in a Tibetan semi-arid alpine steppe during growing seasons of 2013 and 2014. Our results showed that warming decreased seasonal Re, Rh and Ra by 29%, 37% and 13%, respectively. However, warming tended to increase the contribution of Ra to Re (Ra/Re) but decrease that of Rh to Re (Rh/Re). Negative responses of Re was closely related to the changes in plant biomass and soil microbial biomass carbon. The apparent $Q_{10}$ values of Ra were higher than those of Re and Rh, with the $Q_{10}$ values ranked as Ra > Re > Rh. Warming decreased the apparent $Q_{10}$ values of Re and the two components. Our results emphasize that Re and its components respond negatively to experimental warming, and soil carbon loss has the potential to be less under future climatic warming in the Tibetan semi-arid alpine steppe.

## 1. Introduction

Global mean air temperature has increased by approximately 0.85 °C since the industrial revolution and it is predicted to rise more rapidly in the coming decades (IPCC, 2013). In alpine regions, especially on the Tibetan Plateau, the magnitude of warming is predicted to be much greater than the global average (Yang et al., 2014; Pepin et al., 2015; Kuang and Jiao, 2016). Owing to extremely harsh natural environment and magnitude of soil carbon stocks, the Tibetan alpine grasslands are assumed to be particularly vulnerable to climate change (Yang et al., 2008; Chen et al., 2013). A growing number of evidences have shown that climate warming can dramatically alter the structure and function of alpine grasslands (Ding et al., 2016; Liu et al., 2018), and these warming-induced changes in ecosystem processes are expected to have substantial impacts on carbon flux in alpine ecosystems (Hu et al., 2016; Chen et al., 2016; Zhao et al., 2018). The enormous stores of carbon in alpine grasslands soil, which if released into the atmosphere, will be likely to lead to a positive feedback on climate warming (Chen et al., 2016; Bosch et al., 2017). However, studies about how alpine ecosystems carbon flux response to climatic warming still limited, especially in the Tibetan semi-arid alpine grasslands, which could increase the uncertainties for us to accurate evaluate the impact of climate warming on carbon cycles in alpine ecosystems (Wang et al., 2014; Chen et al., 2016).

Ecosystem respiration (Re) represents the largest carbon fluxes in terrestrial cycle (Cox et al., 2000; Davidson et al., 2006), greatly regulated by soil temperature, soil moisture, and substrate supply (Lin et al., 2011; Hu et al., 2016; Zhao et al., 2018). Small warming-induced fluctuations in Re are expected to lead to pronouncing variation in atmospheric $CO_2$ (Welker et al., 2004; Heimann and Reichstein, 2008). The potential effects of experimental warming on Re have been examined in a variety of grassland ecosystems (Li et al., 2013; Wang et al., 2014; Chen et al., 2017; Fang et al., 2018). Previous meta-analyses have reported that experimental warming generally increased Re in grassland ecosystems mainly due to warming-induced increasing in plant biomass, litter decomposition and microbial activity (Rustad et al.,

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2001; Lu et al., 2013; Wang et al., 2014). However, the effects of elevated temperature on Re have been highly variable in individual studies (Chen et al., 2016; Zou et al., 2018). In grasslands ecosystems, experimental warming can largely decrease soil surface moisture due to enhanced evaporation, and the stimulating effects of increased temperature on Re might be offset when soil water becomes a limiting factor (Bradford et al., 2009; Flanagan et al., 2013). Especially in the water-limited grassland ecosystems, where soil temperature and moisture both were critical environmental factors determining the physiology of vegetation and soil microbial activities (Liu et al., 2009; Chimner et al., 2010; Wang et al., 2014; Li et al., 2017), the warming-induced moisture stress tended to significantly decrease plant biomass and suppressed microbial activity, and consequently lead to decrease of Re (Wu et al., 2011; Liu et al., 2016). In addition, total Re is an integrated result of autotrophic respiration (Ra) and heterotrophic respiration (Rh), the two components of Re generally response to climate change in complex ways (Li et al., 2013; Chen et al., 2016). Recent meta-analysis suggested that Rh and Ra showed different responses to experimental warming (Wang et al., 2014). Such differential responses in the Rh and Ra could be largely related to the disparity results of Re under experimental warming (Lu et al., 2013; Wang et al., 2014). Thus, it is crucial to distinguish Rh and Ra for better understanding and evaluating the role of Re in the global C cycle under climate warming.

The Tibetan Plateau has experienced more rapid climate warming in recent decades (Yang et al., 2014; Kuang and Jiao, 2016). By the end of 21st century, it is projected that annual mean temperature and precipitation on the Tibetan Plateau will increase by 2.8–4.9 °C and 15–21%, respectively (Gao et al., 2014). Since temperature is a key driver of ecosystem biogeochemical processes, on-going warming on the Tibetan Plateau will be likely to remarkably affect carbon cycles in alpine grasslands (Saito et al., 2009). Some simulation experiments have been conducted to examine the potential responses of Re to climate warming in Tibetan alpine grasslands, and Re has been reported increased (Hu et al., 2016; Chen et al., 2017), decreased (Fu et al., 2013) and not changed (Lin et al., 2011; Chen et al., 2016) in alpine grasslands under experimental warming. These inconsistent responses of Re in alpine grasslands might be largely due to differential responses of Ra and Rh to experimental warming (Chen et al., 2016). However, in alpine grasslands, only a few studies focused on the effects of increased temperature on the two components of Re, and these previous studies found that Rh and Ra respond divergent to experimental warming (Wang et al., 2014; Peng et al., 2015; Chen et al., 2016). For example, experimental warming stimulated both Ra and Rh in a permafrost alpine meadow (Peng et al., 2015). Chen et al. (2016) observed that warming enhanced Ra but did not change Rh in a Tibetan alpine meadow. The responses of Re and its two components to warming are rarely studied in water-limited alpine grasslands, particularly in the Tibetan semi-arid alpine steppe, there remains a lack of information about a comprehensive mechanistic understanding of Re and its two components response to warming in alpine grassland ecosystems.

The alpine steppe ecosystem usually suffered water deficits due to high evaporation, experimental warming might further stimulate evaporation and consequently accelerate the dry condition (Zhu et al., 2017). Thus, we hypothesize that warming-induced soil water deficits could constrain both plant growth and soil microbial activity in semi-arid alpine steppe, which might result in decreases of Re and its components. To test the hypotheses, we conducted a manipulative experiment of warming with two treatments (warming, W; control, CK) in a semi-arid alpine steppe on the central Tibetan Plateau. Experimental warming was achieved by a free-air temperature enhancement system with infrared heaters. Growing season Re, Rh, Ra and the related environmental factors were observed during the growing seasons of 2013 and 2014. The main objectives were: (1) to examine the responses of growing season Re and its two components to experimental warming; (2) to examine driving factors of warming on Re, Ra and Rh and (3) investigate the temperature sensitivity of Re and its two components under warming.

## 2. Materials and methods

### 2.1. Study site

The study was conducted at the Nam Co Station for Multisphere Observation and Research, Chinese Academy of Sciences (30°46′N, 90°59′E; 4730 m a.s.l.), which was located at the northern slope of the Nyainqentanglha Mountains on the central Tibetan Plateau. The climate is characterized by semi-arid alpine monsoon, with annual mean ambient temperature around −0.6 °C, annual precipitation of 414.6 mm, and annual pan evaporation of 1726 mm (Wei et al., 2014). More than 80% of the annual precipitation occurs in the growing season (May to September). During 1963–2010, annual mean temperature increased by 1.6 °C while annual precipitation showed a slight increasing trend (Wang et al., 2013; Zhao et al., 2016). The major vegetation type in the study site is alpine steppe dominated by *Stipa purpurea* and *Kobresia pygmaea*, with the vegetation height < 10 cm and about 95% of root biomass appearing at the top 30 cm of soil (0–10 cm, 50%; 10–20 cm; 30%; 20–30 cm, 15%; 30–50 cm, 5%). Vegetation cover was about 30–40% in the alpine steppe ecosystem, in which the coverage of *Stipa purpurea* and *Kobresia pygmaea* were about 5–13% and 4–11%, respectively. Other coexisting plant species included *Oxytropis glacialis*, *Potentilla saundersiana*, *Poa annua*, *Saussurea japonica*, *Androsace tapete* and *Arenaria pulvinata*. The grassland turns green at the end of April or the beginning of May and the above ground biomass typically reaches its maximum volume in late July or August (Liu et al., 2013). The soil is a typical alpine steppe soil characterized by very low clay content, with 80% sand and 2.5% organic matter within the surface soil horizons (Zhu et al., 2015). Before the initiation of the experiment (in 2012), the soil samples from the study site were collected and analyzed, with soil properties as follows: soil total organic carbon 35.26 g/kg, soil total nitrogen 2.83 g/kg, total phosphorus 0.49 g/kg, $NH_4$–N, 4.25 mg/kg, $NO_3$–N, 6.94 mg/kg.

### 2.2. Experimental design

The experiment was manipulated using as a paired design with two levels of temperature treatment (+0 °C and + 2 °C above ambient, i.e. CK vs warming). Each treatment was replicated in four blocks with a distance of 3 m between adjacent blocks. In each of the four blocks, two paired plots (1.2 m × 2.4 m) were set up for the two treatments with 2-m buffer between each adjacent plot. In total, 8 treatment plots were established. In each warming plot, two infrared lamps (GHT220-800, Beijing Sanyuan Huahui Electric Light Source Co. Ltd., Chaoyang, Beijing, China) were installed on two iron frames standing at both shorter sides of the plot, evenly emitting heat to the ground in an inclination angle of 45° and at a height of 1.3 m above the ground. The infrared lamps were controlled by an automatic temperature control system (IDAQ-8098, Shenzhen Advcom Electronic Technology Co. Ltd., Shenzhen, Guangdong, China). The set-point difference of surface temperatures between warming and CK plots was +2.0 °C during the growing season (from May to September). All the warming plots were heated 24 h per day during the growing seasons of 2013–2014. Soil temperature and volumetric soil moisture at −5 cm for each treatment were measured with HOBO weather stations (Onset Inc., Bourne, MA, USA), which were recorded at 30-min interval.

### 2.3. Measurements of ecosystem respiration and its components

One year before the respiration measurements (in 2012), deep polyvinyl chloride (PVC) collars (diameter: 20 cm; height: 50 cm) were inserted into the soil with 2 cm remaining above the surface of the grass floor for measuring Rh at each plot. Living plants were removed as soon as these deep PVC collars insertions. The deep PVC collars can cut off

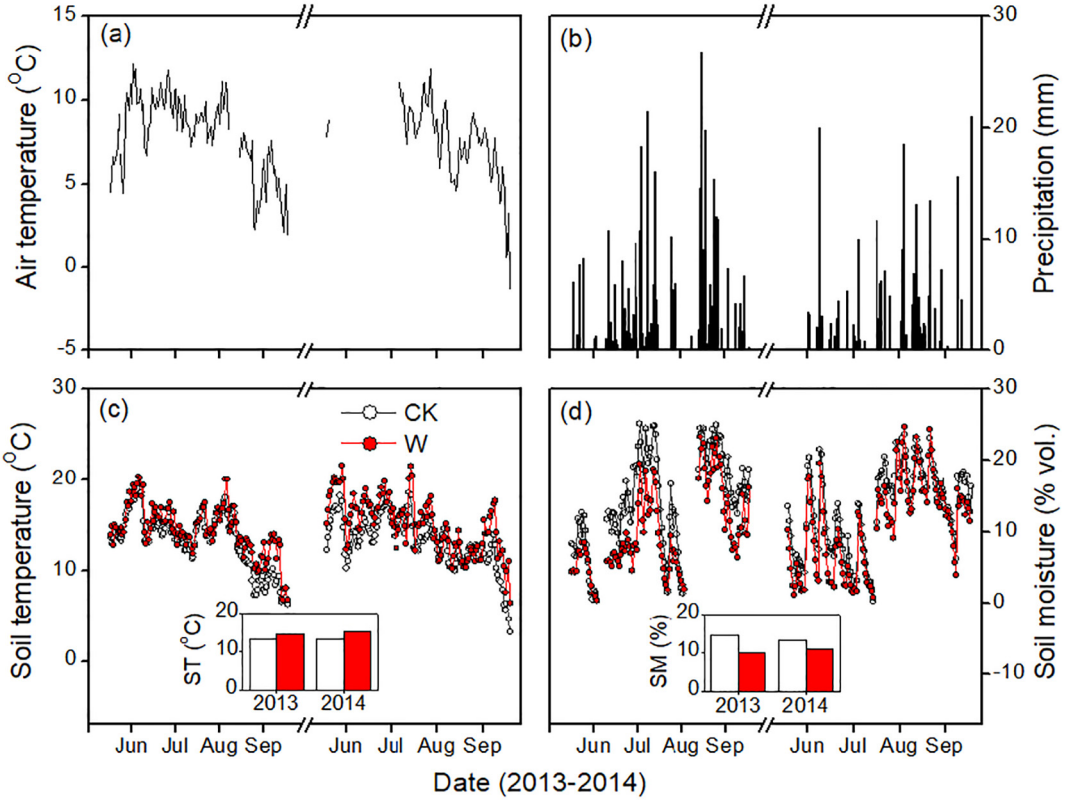


**Fig. 1.** Seasonal variations in (a–b) daily mean air temperature and precipitation, (c–d) daily mean soil temperature and moisture under control (CK) and warming (W) treatments.

the old plant roots and prevented new roots from growing inside the collars. In addition, a shallow PVC collar (diameter: 20 cm; height: 5 cm) was placed with 2 cm remaining above the surface of the grass floor at each treatment plot for measuring Re. On sunny days during the growing season (June to September), Re and Rh were measured (10:00–11:00, local time) twice a month in 2013 and 2014 using the opaque chamber of Li-8100 103 automatic soil $CO_2$ flux system (LI-COR Biosciences, Lincoln, NE, USA). The Ra values were calculated as the difference between Re and Rh. To determine the differences in soil temperature (ST), soil moisture (SM) and the temperature sensitivity of Re and its components ($Q_{10}$) between warming and control treatments, a digital temperature sensor (Type E, OMEGA Engineering, Inc., Stamford, CT, USA) and a Time Domain Reflectometer with a handheld push probe (Type ML2x, Delta-T Devices Ltd, Burwell, Cambridge, United Kingdom), which were attached to the Li-8100 system , were used to measure ST and volumetric SM of −5 cm at each collar.

### 2.4. Measurements of plant biomass and soil propriety

In the central of each treatment plot (1.2 m × 2.4 m), we set a 50 × 50 cm quadrat. In each quadrat, species composition and species-specific maximum plant cover and height were observed in mid-August of 2013–2014. The above part of the plant was harvested to estimate aboveground biomass (AGB) in each quadrat. The belowground biomass (BGB) was estimated through collecting five soil cores in each quadrat (diameter: 5.0 cm; depth: 30 cm) and washing off the soil by a 2-mm sieve. Both the AGB and BGB samples were dried at 65 °C for 48 h and weighed. We collected top soil samples (0–10 cm in depth) with a soil auger (diameter: 3.0 cm) from each quadrat. After removal of visible roots, soil samples were air-dried at room temperature and sieved for measuring soil properties. Soil organic carbon (SOC) was determined by the Walkley and Black potassium dichromate oxidation method (Nelson and Sommers, 1982). Soil microbial biomass carbon (MBC) was measured using the fumigation extraction method (Roscoe and Buurman, 2003).

### 2.5. Statistical analysis

Independent sample *t*-tests were used to test the differences in AGB, BGB, SOC, MBC, Re, Ra and Rh between warming and CK treatments. Repeated-measures ANOVA analyses were used to test the effects of date, warming, and their interaction on Re and its components at each year.

The temperature sensitivity ($Q_{10}$) of Re, Ra and Rh during the growing season was calculated according to the Van't Hoff equation (Lloyd and Taylor, 1994):

$$R = \alpha e^{bT},$$

in which $Q_{10}$ was calculated as:

$$Q_{10} = e^{10b}.$$

where, R is respiration, $\alpha$ is the intercept of respiration when $T$ is 0 °C and $b$ reflects the temperature sensitivity of respiration.

The warming-induced relative differences in AGB, BGB, SOC, Re, Ra and Rh were calculated as:

$$\text{Relative differences (\%)} = 100 \times (\text{Warming} - \text{CK})/\text{CK}.$$

All statistical analyses were performed using SPSS 18.0 (SPSS Inc., Chicago, Illinois, USA), and all significant differences were taken at $P < 0.05$.

## 3. Results

### 3.1. Variation in microclimate

Air temperature and precipitation showed a clear seasonal pattern,

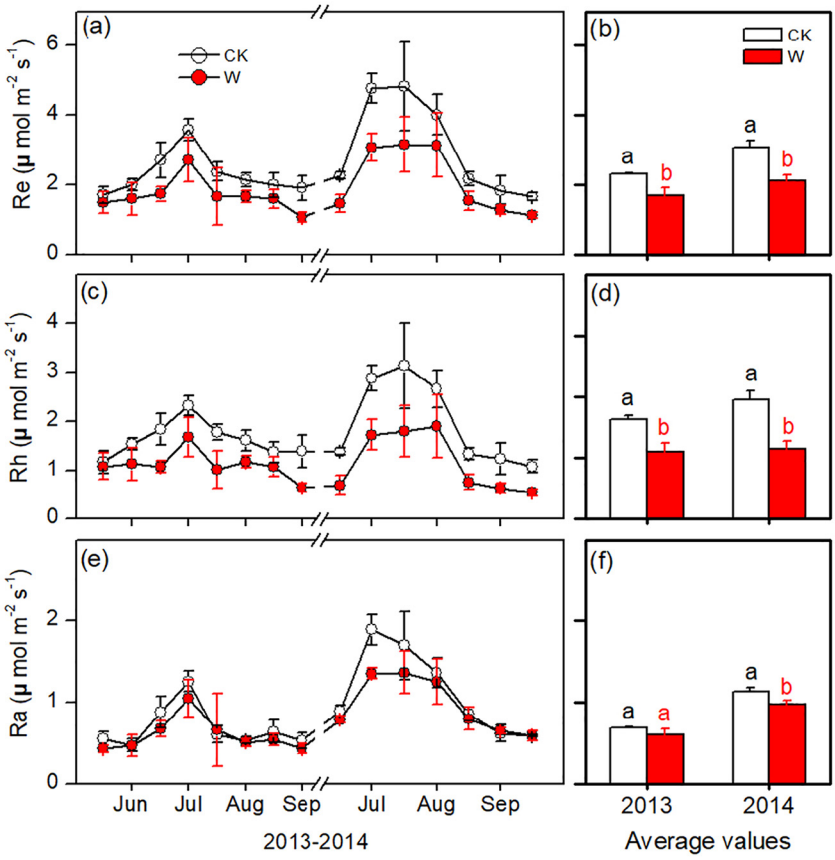


**Fig. 2.** Seasonal variations and growing season average value of (a and b) ecosystem respiration (Re), (c and d) heterotrophic respiration (Rh) and (e and f) autotrophic respiration (Ra) in semi-arid alpine steppe in 2013 and 2014. Different letters indicate a significant difference between warming (W) and control (CK) treatments at $P < 0.05$. Bars indicated SE of mean, $n = 4$.

and daily mean air temperature was generally > 0 °C over the growing season (June to early September), while most of the precipitation events concentrated in the season of mid-June to mid-August (Fig. 1a–b). Seasonal patterns in soil temperature (Ts, Fig. 1c) and moisture ($M_s$, Fig. 1d) across different treatments were associated with the variations of air temperature and precipitation in the ambient environment (Fig. 1a–b). Warming treatments significantly increased soil temperature (ST) compared with that of the controls. Mean ST at the depth of 5 cm during the study period was 1.2–1.8 °C higher in the warming plots than that in the control plots (Fig. 1c). However, warming decreased volumetric soil moisture (SM) by 17–32% compared with the control plots (Fig. 1d).

### 3.2. Effect of warming on Re and its components

There were comparable seasonal patterns of the Re and its two components across experimental treatments, with Re, Ra and Rh values peaking in July for both control and warming treatments (Fig. 2a–d). We also observed that 2-year average Re and its two components significantly decreased under warming, with the seasonal average Re, Rh and Ra decreased by 29%, 37% and 13% over the two growing seasons, respectively (Fig. 2a–d and Table 1). Briefly, negative responses of Re and Rh were found in both 2013 and 2014 (Fig. 2a–d and Table 2). However, we only found the negative warming effect on Ra only in 2014 rather than 2013 during the experiment periods (Fig. 2e–f and Table 2). No significant interactions between measure years and warming treatments were found for Re, Rh and Ra (Table 2). The contribution of Rh to Re (Rh/Re) and Ra to Re (Ra/Re) also varied greatly between control and warming treatments (Fig. 3a–b). The Rh/Re ratio in the control and warming treatments was in the range of 63–70% and 54–65%, with a mean of 67% and 60%, respectively (Fig. 3a–b). The average Ra/Re ratio was 33% and 40% in control and warming treatments, respectively (Fig. 3a–b). Warming significantly

**Table 1**
Results (F values) of two-way ANOVA analyses for measuring year (Y), warming (W), and their interaction on ecosystem respiration (Re), heterotrophic respiration (Rh) and autotrophic respiration (Ra).

| Effects | Re | Rh | Ra |
|---|---|---|---|
| Warming (W) | 65.181*** | 93.013*** | 14.044** |
| Year (Y) | 37.713*** | 7.400* | 159.356*** |
| W × Y | 3.408 | 4.308 | 1.200 |

Significant levels.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

**Table 2**
Results (F values) of repeated-measures ANOVA analyses for measuring data (D), warming (W), and their interaction on ecosystem respiration (Re), heterotrophic respiration (Rh) and autotrophic respiration (Ra) during the growing seasons of 2013 and 2014.

| Year | Effects | Re | Rh | Ra |
|---|---|---|---|---|
| 2013 | Warming (W) | 30.114*** | 51.069*** | 3.586 |
| | Date (D) | 10.919*** | 8.252*** | 12.968*** |
| | W × D | 0.748 | 1.475 | 0.514 |
| 2014 | Warming (W) | 33.221*** | 47.854*** | 8.304** |
| | Date (D) | 27.979*** | 23.653*** | 35.141*** |
| | W × D | 1.275 | 1.024 | 1.961 |

Significant levels.
** $P < 0.01$.
*** $P < 0.001$.

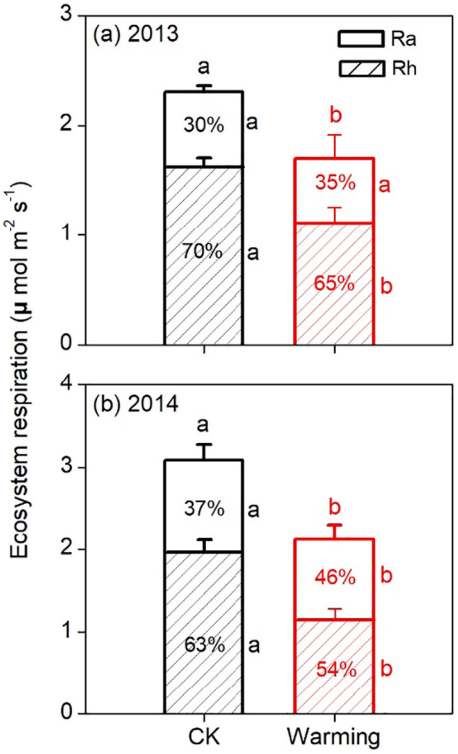


**Fig. 3.** The contribution of heterotrophic respiration (Rh) and autotrophic respiration (Ra) to total ecosystem respiration in (a) 2013 and (b) 2014 under control (CK) and warming (W). Different letters represent significant difference at $P < 0.05$. Bars indicated SE of mean, $n = 4$.

decreased the Rh/Re by 11% whereas tended to increase Ra/Re by 22%, respectively (Fig. 3a–b).

### 3.3. Factors effecting Re and its components to warming

We found that both ST and SM could well explain the seasonal variation of Re and its components (Fig. 4a–c). The seasonal Re, Ra and Rh showed an exponential response to ST. In addition, linear regression analyses showed that Re, Ra and Rh were significantly affected by SM for both the control and warming treatments. Experimental warming significantly decreased MBC, but had no significant effect on AGB, BGB and SOC in both 2013 and 2014 (Fig. 5e–h). The growing season Re, Ra, and Rh were significant correlated with AGB, but showed no significant correlation with SOC (Table 3). Seasonal Re and Rh were greatly related to MBC (Table 3). Compared to the CK treatment, warming-induced differences in Re and Rh rather than Ra was mainly related to that of AGB, BGB and MBC (Fig. 5a–c). However, we found no significant relationships between warming-induced differences in Re, Rh, Ra and that of SOC (Fig. 5c).

### 3.4. Temperature sensitivity of Re and its components

On the seasonal scale, we found that Re, Ra and Rh were positively correlated with ST for both the control treatments and warming treatments (Fig. 4). The $Q_{10}$ value of Ra was higher than that of Re and Rh, with $Q_{10}$ values ranked as Ra > Re > Rh for both control and warming treatments (Table 4). At the same time, experimental warming had significant negative effects on the temperature sensitivity of Re, Ra and Rh, with the apparent $Q_{10}$ values of Re and its components decreased significantly under warming (Table 4).

## 4. Discussion

### 4.1. Warming effects on Re and its components

Previous studies have shown that Re is greatly regulated by soil temperature, soil moisture, and substrate supply in alpine grassland ecosystems (Lin et al., 2011; Hu et al., 2016; Zhao et al., 2018). We found that experimental warming had a negative effect on growing season average Re in Tibetan semi-arid alpine steppe (Fig. 2a–d), which was in line with previous studies in the same grassland ecosystems (Fu et al., 2013; Zhao et al., 2018) but contrary to some previous studies in other alpine grasslands (Lin et al., 2011; Chen et al., 2016; Hu et al., 2016; Chen et al., 2017). Generally, net responses of Re to experimental warming could be a combination warming effects on Ra and Rh. However, in grassland ecosystems, experimental warming generally caused contrary responses of Ra versus Rh due to the differences of biotic and abiotic factors between eco-regions (Lu et al., 2013; Wang et al., 2014; Chen et al., 2016). Peng et al. (2015) have reported that experimental warming stimulated both Ra and Rh in a permafrost alpine meadow. Chen et al. (2016) observed that warming enhanced Ra but did not change Rh in a Tibetan alpine meadow. To our knowledge, this is the first investigation about the responses of Re and its two components to experimental warming in a Tibetan semi-arid alpine steppe. We found that warming decreased the growing season Re, Rh and Ra (Fig. 2a–f). Given that soil water condition is a key factor in controlling plant productivity and microbial activities as well as soil physicochemical properties (Wan et al., 2007; Liu et al., 2009), the response of Re to experimental warming could be regulated by soil water available in alpine grassland ecosystems (Wu et al., 2011; Liu et al., 2016). Especially for the alpine steppe, which is generally water-limited and sensitive to changes in precipitation, warming-induced soil drying was considered as a major reason for the decline of Re (Fu et al., 2013). Warming caused soil water deficit could decrease soil and litter decomposition rate and suppress soil enzyme and microbial activity, consequently resulting in a decrease of Rh (Link et al., 2003; Zhu et al., 2015). In the present study, warming decreased MBC but had no significant effects on SOC content (Fig. 5e–h), which suggested that warming-induced changes in soil microbial activity rather than SOC decomposition could be a major reason for the decrease in Rh. However, experimental warming caused changes in the proportions of labile versus recalcitrant carbon might also result in the complex responses of Rh to experimental warming (Bradford et al., 2009). In the alpine grassland ecosystems, most of the plant roots are close to the surface, and plant biomass is a major contributor to Re (Zhang et al., 2009). Previous studies suggested that Ra is expected to be more sensitive to environmental factors (Lin et al., 2011; Chen et al., 2016). Due to the importance of plant growth in respiratory processes, warming caused changes in plant biomass could directly reduce Ra and indirectly reduce Rh through decreasing respiratory substrate supply (Wan et al., 2007). However, in the present study, experimental warming had no significant effects on both aboveground and belowground part of plant biomass (Fig. 5e–f), suggesting that warming-induced changes in Ra might be less compared with that of Rh. As reported by the previous studies, Rh is the most contributor to the total Re in the alpine grasslands (Peng et al., 2015; Chen et al., 2016), we attribute the warming-induced reduction in Rh as the major source of the decrease in Re. In consideration of the rapid climate warming on the Tibetan Plateau in recent decades (Yang et al., 2014; Kuang and Jiao, 2016), our results further emphasized that the soil carbon loss has the potential to be less under future climate warming in the Tibetan semi-arid alpine steppe.

### 4.2. Warming effects on the contribution of Rh and Ra to Re

The root exclusion method has been widely used for partitioning total Re into Rh and Ra in many grassland ecosystems (Li et al., 2013; Chen et al., 2016; Ren et al., 2016; Zeng et al., 2016). In alpine

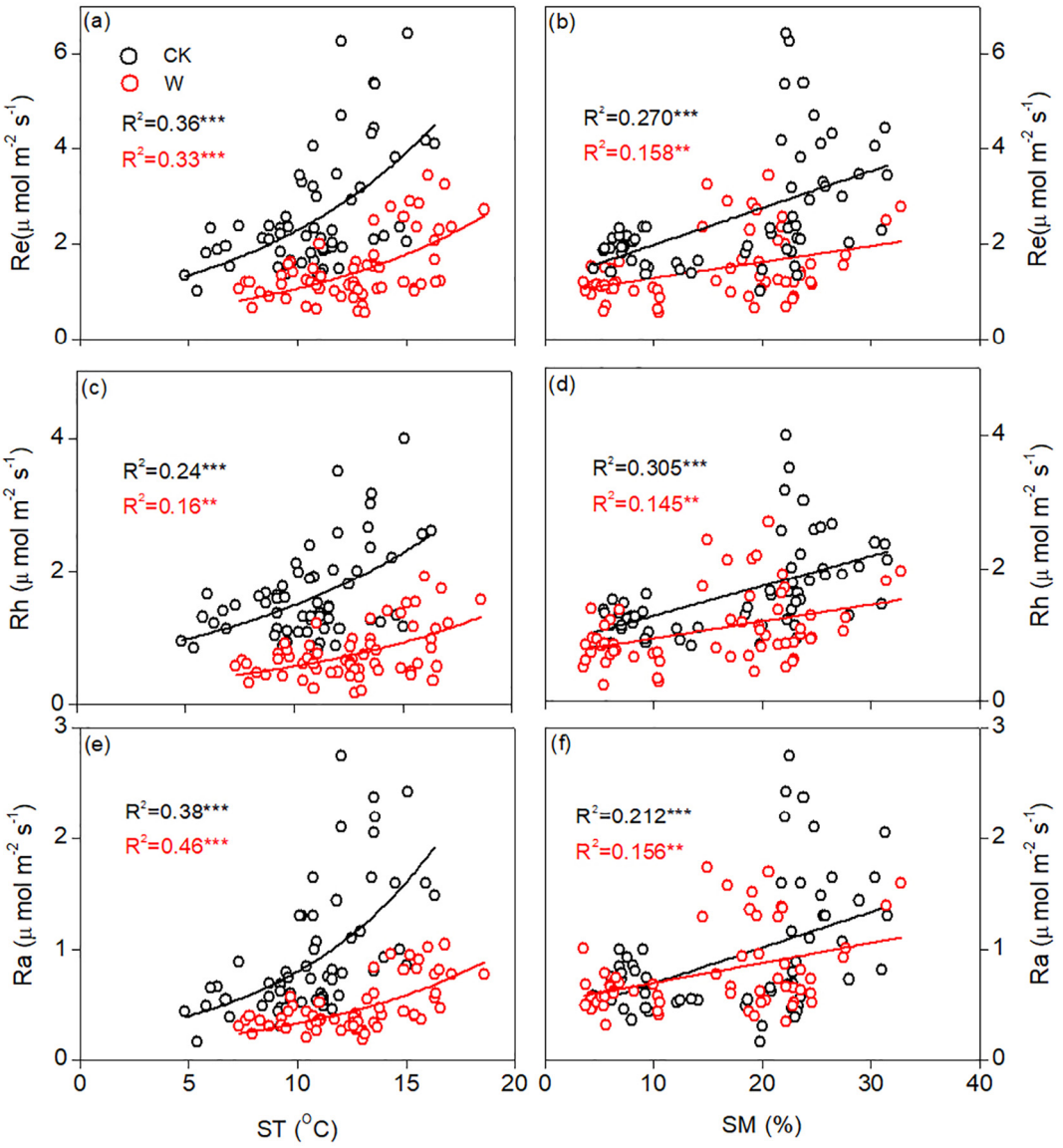


**Fig. 4.** Relationships of (a and b) ecosystem respiration (Re), (c and d) heterotrophic respiration (Rh) and (e and f) autotrophic respiration (Ra) with soil temperature (ST) and soil moisture (SM) in three alpine grasslands based on the observations under warming (W) and control (CK) treatments in 2013 and 2014. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

grassland ecosystems, such root exclusion method has already been successfully used to distinguish Re into Rh and Ra (Peng et al., 2015; Chen et al., 2016; Ren et al., 2016). However, previous studies suggested that root exclusion method may cause uncertainty in estimating Ra and Rh (Ngao et al., 2007; Bond-Lamberty et al., 2011; Chen et al., 2016; Fang et al., 2018). For example, root exclusion methods could result in a transient increase of Re due to the decomposition of dead roots and the variation of microbial community (Fang et al., 2018). Some reported studies also noted that root exclusion methods resulted in underestimation of Rh owing to the exclusion of substrate input from dead roots and root exudates (Ngao et al., 2007; Li et al., 2013). In alpine grasslands, most of the plant roots are close to the surface, and the majority of root biomass is found at the top soil (Wang et al., 2013; Zhao et al., 2018). In the present study, about 95% of root biomass appearing at the top 30 cm of soil. The 50-cm-deep collars are long enough for excluding most living roots effective for partitioning the total Re into Rh and Ra in alpine grassland ecosystems (Peng et al., 2015; Chen et al., 2016). In addition, deep collars were inserted into soil approximately one year before the observation started, that the effect of dead root decomposition on Rh might have been minimized.

Regardless of the experimental treatments, our results showed that the average contribution of Rh to Re (Rh/Re) and Ra to Re (Ra/Re) were 63% and 37%, respectively (Fig. 3a–b). The proportions of Ra and Rh components to Re were within the ranges of results reported by the previous studies (Fu et al., 2011; Peng et al., 2015; Cheng et al., 2016; Ren et al., 2016), which indicate that any biases caused by the root exclusion method can be probably minor in the present study. In the alpine grassland ecosystems, Ra is greatly correlated with plant biomass and substrate availability (Zhang et al., 2009; Zhao et al., 2017). We attribute the relatively lower Ra/Re ratio than Rh/Re ratio partly due to the lower plant biomass and litter production in the semi-arid alpine steppe (Zhao et al., 2016). The fact that Rh/Re was relatively larger than Ra/Re (Fig. 3a–b), indicating that changes in microbial activities rather than plant biomass might play more important roles in affecting Re in the Tibetan semi-arid alpine steppe. The semi-arid alpine steppe usually suffered water deficits due to high evaporation, experimental warming might further stimulate evaporation and consequently accelerate the dry condition (Zhu et al., 2017). Warming-induced soil water deficits could constrain soil microbial activity in semi-arid alpine steppe, which might directly result in decreases of Rh. In the present

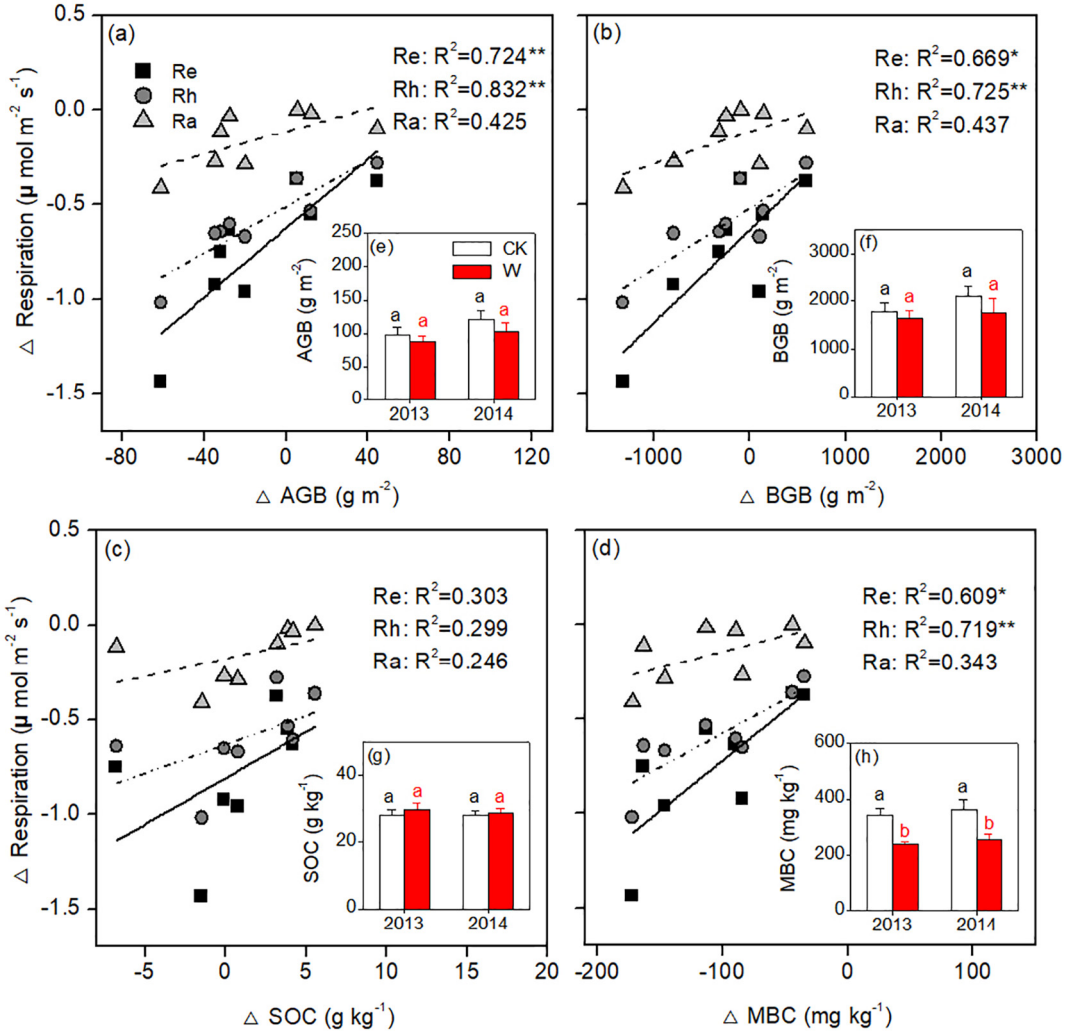


**Fig. 5.** Relationships of warming induced differences in ecosystem respiration (Re), heterotrophic respiration (Rh) and autotrophic respiration (Ra) with (a) differences in aboveground biomass (AGB), (b) differences in belowground biomass (BGB), (c) differences in soil organic carbon (SOC) and (d) differences in microbial carbon biomass (MBC). Effects of experimental warming on (e) AGB, (f) BGB, (g) SOC and (h) MBC in semi-arid alpine steppe. Different letters indicate a significant difference between warming (W) and control (CK) treatments. Relative differences (Δ, %) = 100 × (W − CK) / CK. Asterisks denote a significant difference between warming and control treatments. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Bars indicated SE of mean, $n = 4$.

**Table 3**
Correlation coefficients of the Pearson correlations among ecosystem respiration (Re), heterotrophic respiration (Rh), autotrophic respiration (Ra), aboveground biomass (AGB), belowground biomass (BGB), soil organic carbon (SOC), microbial biomass carbon (MBC).

| | Re | Rh | Ra |
|---|---|---|---|
| AGB | 0.600* | 0.529* | 0.544* |
| BGB | 0.502* | 0.471 | 0.408 |
| SOC | 0.047 | 0.051 | 0.033 |
| MBC | 0.625** | 0.732** | 0.265 |

Significant levels.
* $P < 0.05$.
** $P < 0.01$.

study, experimental warming significantly affected the contributions of the two components, with a result of increases in Ra/Re ratio but decreases in Rh/Re ratio in the Tibetan semi-arid alpine steppe (Fig. 3a–b). As Ra values were calculated as the difference between Re and Rh, warming-mediated reduction of Re could be mainly associated with a decrease in Rh in the Tibetan semi-arid alpine steppe.

**Table 4**
The $Q_{10}$ values of ecosystem respiration (Re), heterotrophic respiration (Rh) and autotrophic respiration (Ra) under control and warming treatment. Different letters indicate a significant difference among the $Q_{10}$ values of Re, Rh and Ra ($P < 0.05$). Asterisks denote a significant difference between control and warming treatments. Values in parentheses indicated SE of mean, $n = 8$.

| Model | Re | Rh | Ra |
|---|---|---|---|
| Control | 2.62 (0.32)a | 2.18 (0.19)a | 3.64 (0.64)a |
| Warming | 2.41 (0.16)ab | 1.96 (0.16)a | 3.00 (0.17)b* |

* $P < 0.05$.

### 4.3. Temperature sensitivity of Re and its components

The $Q_{10}$ value is an important parameter used to assess the temperature sensitivity of Re and its components (Qi and Xu, 2001; Davidson et al., 2006). In the present study, the $Q_{10}$ values (on average, 2.51 for Re, 2.07 for Rh and 3.32 for Ra) fall within the ranges reported by previous studies in alpine grasslands (Peng et al., 2009; Lin et al., 2011; Fu et al., 2013; Zhao et al., 2017). We found that the apparent $Q_{10}$ values ranked as Ra > Re > Rh (Table 4), a trend in line with other studies (Lin et al., 2011; Hu et al., 2016; Zou et al., 2018). The

higher $Q_{10}$ values for Ra than Rh could have mainly resulted from the relative higher seasonal variations in plant biomass than that of soil carbon (Zou et al., 2018). Thus, in Tibetan semi-arid alpine grasslands, our results indicated that Re might be most sensitive to climate warming if plant biomass contributes most portion of the total ecosystem carbon emissions. Previous studies have reported variable responses of $Q_{10}$ to experimental warming in alpine grassland ecosystems, with the $Q_{10}$ increased (Hu et al., 2016) or decreased (Lin et al., 2011; Zhao et al., 2018) under warming. In the present study, experimental warming tended to decrease $Q_{10}$ of Re and its components (Table 4). Generally, the $Q_{10}$ values are mainly affected by temperature range, soil moisture and substrate availability in grasslands (Peng et al., 2009; Wan et al., 2007). We attributed the warming-induced decrease in $Q_{10}$ values of Re mainly to the modification effects of soil moisture. The semi-arid alpine steppe usually suffered water deficits due to high evaporation, and warming could result in desiccation stress of the rhizosphere or soil microorganisms, which might decrease $Q_{10}$ of Ra and Rh (Wagle and Kakani, 2014). In addition, the reduction in $Q_{10}$ of Ra and Rh also could be attribute to a direct physiological acclimation of the plants respiration or microorganisms' activities to warming (Luo et al., 2001; Atkin and Tjoelker, 2003). Moreover, experimental warming could cause changes in soil microbial community (Rui et al., 2015; Zhang et al., 2016), and might consequently lead to changes in $Q_{10}$ values in alpine grasslands, which deserved further studies.

## 5. Conclusions

Our results suggested that a warming-mediated decrease in seasonal Re, Rh and Ra occurred in a Tibetan semi-arid alpine steppe. However, warming tended to increase the contribution of Ra to Re (Ra/Re) but decrease that of Rh to Re (Rh/Re). The reduced Re was closely related to the warming-caused changes in AGB, BGB and MBC. In addition, experimental warming also had negative effects on temperature sensitivity of Re, Ra and Rh. The apparent $Q_{10}$ values of Ra were higher than that of Rh, suggested that the responses of Ra to soil temperature was more sensitive than that of Rh. Our findings emphasized that experimental warming have negative effects on Rh and Ra, and consequently the carbon loss has the potential to resist climate warming in semi-arid alpine steppe on the Tibetan Plateau.

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